THE PHYLOGENIC RELATIONSHIP OF *LYSTROSAURUS* TO CONTINENTAL DRIFT WITH A DESCRIPTION OF AN ANTARCTIC *LYSTROSAURUS*

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INTRODUCTION

The affinities of modern land-living animals are intimately related to the positions and connections of continents. The relationship between continental positions and tetrapod faunas (paleozoogeography) is reflected by the distributions of extinct amphibians and reptiles during Paleozoic and Mesozoic eras. The early Triassic Lystrosaurus fauna, an example of such a distribution, originally described from South Africa, is now known in Antarctica, in peninsular India, and in western China. The distributions of this ancient tetrapod fauna indicate that the regions in which they now occur were then intimately associated, allowing for intermigrations of land-living vertebrates. As such, these occurrences lend strong support to the theory of Gondwanaland, which supposes the southern hemisphere continents plus peninsular India to have been joined into a single supercontinent (the correlative theory of Laurasia supposes a similar connection of the northern hemisphere continents), and to the theory of continental drift, which visualizes the eventual fragmentation of these supercontinents, the fragments drifting through time to positions occupied by the modern continents.

In any consideration of the Gondwanaland relationships, the genus Lystrosaurus manifests itself by its remarkable abundance. Indeed, so overwhelmingly prevalent is Lystrosaurus within the lowest Triassic sediments of South Africa that its horizon is generally designated as the Lystrosaurus Zone of the Beaufort Series. A similar relation, although not to the same degree as that in South Africa, can be found in Antarctica, India, and China. With such an abundant fossil form, it becomes advantageous to make an investigation into the development of the generic form and its subsequent relation to its environment and the faunal relationship derived from such an environment. These parameters must be conducive to the theory of continental drift in order

for the theory to be effective. What follows is a consideration of the general features of continental drift, a summary of the development of the many forms culminating in the eventual forms of Lystrosaurus recognized today, a description of a Lystrosaurid form, and an evaluation of the manner in which Lystrosaurus complies with the theory of continental drift.

Continental Drift Background

Alfred Wegener is generally and most rightly associated with the formation of the theory of continental drift. However, two people before him made significant suggestions concerning the orientation of continental land masses with time.

Antonio Snider-Pellegrini, with the publication of his La Création et ses mystères dévoilés in 1858, indicated a catastrophic break-up of the Atlantic continents and their subsequent drifting apart. His notion was derived from the idea that, during the cooling and solidifying of the earth, the continental mass formed only on one side, and fracturing and drifting occurred after the Noachian flood, relieving the previous instability. Due to the contemporary Lyellian uniformitarianism, however, such views as Snider's catastrophism were considered beneath the scientific community.

It was not until 1910 that another coherent hypothesis that involved a condition which resembled what we now recognize as continental drift came into being. This paper, by F. B. Taylor, did not deal with the usual idea of the fit of the continents bordering the Atlantic, but rather with the mountain ranges in Eurasia, formed during the Tertiary. He sought an explanation of continental "creep" to resolve the trending of the Himalayas and ranges swinging into Malaysia and Indonesia. Unfortunately, he offered little to explain the mechanisms of continental movement and as such, he had relatively

little impact.

Two years later, in 1912, Alfred Wegener published his book, Die Entstehung der Kontinente. He first examined the opposing coasts of Africa and South America.along the South Atlantic Ocean, pointing out that "not only does the great right-angled bend formed by the Brazilian coast at Cape San Roque find its exact counterpart in the reentrant angle of the African coastline near the Cameroons, but also, south of these two corresponding points, every projection on the Brazilian side corresponds to a similar shaped bay in the African." He then plunged directly into geophysical arguments in order to indicate the inadequacies of the crustal contraction theory. How could such a theory account for the enormous overthrusted nappes in the Alps? And why weren't folds more uniformly distributed over the face of the earth as suggested by a contractile situation? Wegener proceeded to introduce geophysical evidence, such as an isostatic differential between the dichotomous crust material; geological arguments, such as the coastal and stratigraphic similarities on the two sides of the Atlantic; and paleontological evidence, such as the annelida and marsupial distribution, to set forth his hypothesis. The basis of his shifting theory was that the present continents were not fixed through geologic time, but rather that they drifted across the face of the earth to their present positions. According to this theory, the southern-hemisphere continents and India might be the displaced remanents of a great Gondwana continent that broke apart in the geologic past. He, however, evolved no mechanism for his drift theory. Rather he speculated on two components which might power the continental movement. One was a differential gravitational force towards the equator, accepted at the time. The other was some kind of tidal force. Both were critically received (Hallam 1973).

Since the time of this early theory regarding continental drift,

widespread and detailed geophysical and oceanographic work has produced knowledge of the bottom of the sea. These include studies of great ridges running through the lengths of mid-oceanic regions, of deep oceanic trenches bordering various continental blocks, of paleomagnetic measurements that indicate the lateral spreading of the sea floor away from the mid-oceanic ridges, and other paleomagnetic studies that show the former positions of the earthly poles (Bullard 1969, Du Toit 1937, Hallam 1967, Hurley 1968). All of these studies bring evidence to bear on the former positions and relationships of the continents and provide many extensions and ramifications to the theory of continental drift.

However, for a theory to be valid, it must satisfy all aspects upon which it touches. Until a few years ago, many paleontologists felt that the relationships and distributions of former life on earth could be explained without the idea of continental drift. They felt that, given a few land bridges which subsided after the Mesozoic, all faunal and floral similarities could be accounted for. The idea of land-bridge connections across what is now deep ocean seemed to account for the total or nearly identical fossil animals and plants found on different continents. Unless these intercontinental land bridges had existed in the past, similarities of life forms would be in disagreement with Darwinian evolution. As such, isolation of individual gene pools should have given rise to divergence of faunas of the different continents. In essence the drifting of continents raised as many problems as it solved. Those who were most skeptical about the theory were jolted by the discovery (Barrett et al 1968) of a vertebrate fossil in Antarctica, which was shortly thereafter identified as a portion of the lower jaw of a labyrinthodont amphibian. Subsequently, there has been a great deal of fossil material found in the Antarctic region, consisting of a therapsid reptile, Lystrosaurus,

and many related fauna, all of Lower Triassic age (Kitching, Collinson, Elliot, and Colbert 1972). The occurrence of Lystrosaurus in Antarctica, coupled with its occurrence in South Africa, India, and China provides considerable evidence for the support of the continental drift theory. It is important to realize that continental vertebrates are especially reliable indicators of land connections because of their inability to cross major sea barriers. The high degree of comparison of whole faunas between different continents must therefore be accepted as evidence of free land communication. The continental isolation of the distinctive marsupial fauna of Australia gives an excellent example of a rapid development of a group living in absence of the more advanced placentals, thus indicating the fulfillment of an isolated ecological niche, which would indeed be expected with regard to a nondrift paleozoogeographic consideration of fauna relationships. During the Mesozoic, especially in the Triassic, the good fossil record provides a recognizable cosmopolitan fauna, implying a free land communication between all the continents (Hallam 1973). The implications of such a situation as concerns Lystrosaurus will be discussed later.

Given the indications provided by the Lystrosaurian bio-evidence, what were the relations of the great southern continent, Gondwanaland, to the northern supercontinent, Laurasia? It has been found by indepth reconstruction (Dietz and Holden 1970) that the two landmasses formed essentially one immense supercontinent termed Pangea which was surrounded by the universal ocean of Panthalassa: the ancestral Pacific. The fit between North America and Africa provides the principal connection between the future block of northern continents and the future group of southern continents. On the east, the Tethys Sea separated Eurasia from Africa. The present Mediterranean Sea is a remanent of the Tethys. Further evidence for the Tethys is the marine deposits that have

come to be uplifted and folded along a line continuing from southern Europe into the belt of the Himalayas. At the western border of this sea was a connection such that the two continental areas were not completely isolated (fig. 1).

The breakup of Pangea was initiated during the middle of the Triassic period. Two rifts developed, opening up the Atlantic and Indian Ocean by the end of the Triassic. Of the two, the northern rift split Pangea along a line slightly above the equator, creating Laurasia. This rifting also created a vast western inlet which eventually became part of the Gulf of Mexico and the Caribbean Sea (Dietz and Holden 1970). The southern rift split South America and Africa away from the other forms encompassed in Gondwanaland (Antarctica, Australia and India).

During the Jurassic period, those rifts active during the Triassic continued, further widening the Atlantic Ocean and Indian Ocean. At the close of the Jurassic another rift developed, splitting South America from Africa.

By the end of the Cretaceous, the rupture between South America and Africa was complete. At this point, the rifted block began to drift and rotate, such that the motion nearly closed the eastern end of the Tethys Sea. The collision of the Indian peninsula with eastern Asia completes the Mesozoic picture of the continental masses and their associated rifting and drifting. During the Cenozoic, less pronounced changes occurred and, in that they do not enter into discussion of the Lystrosaurian implications of continental drift, they will not be discussed further here.

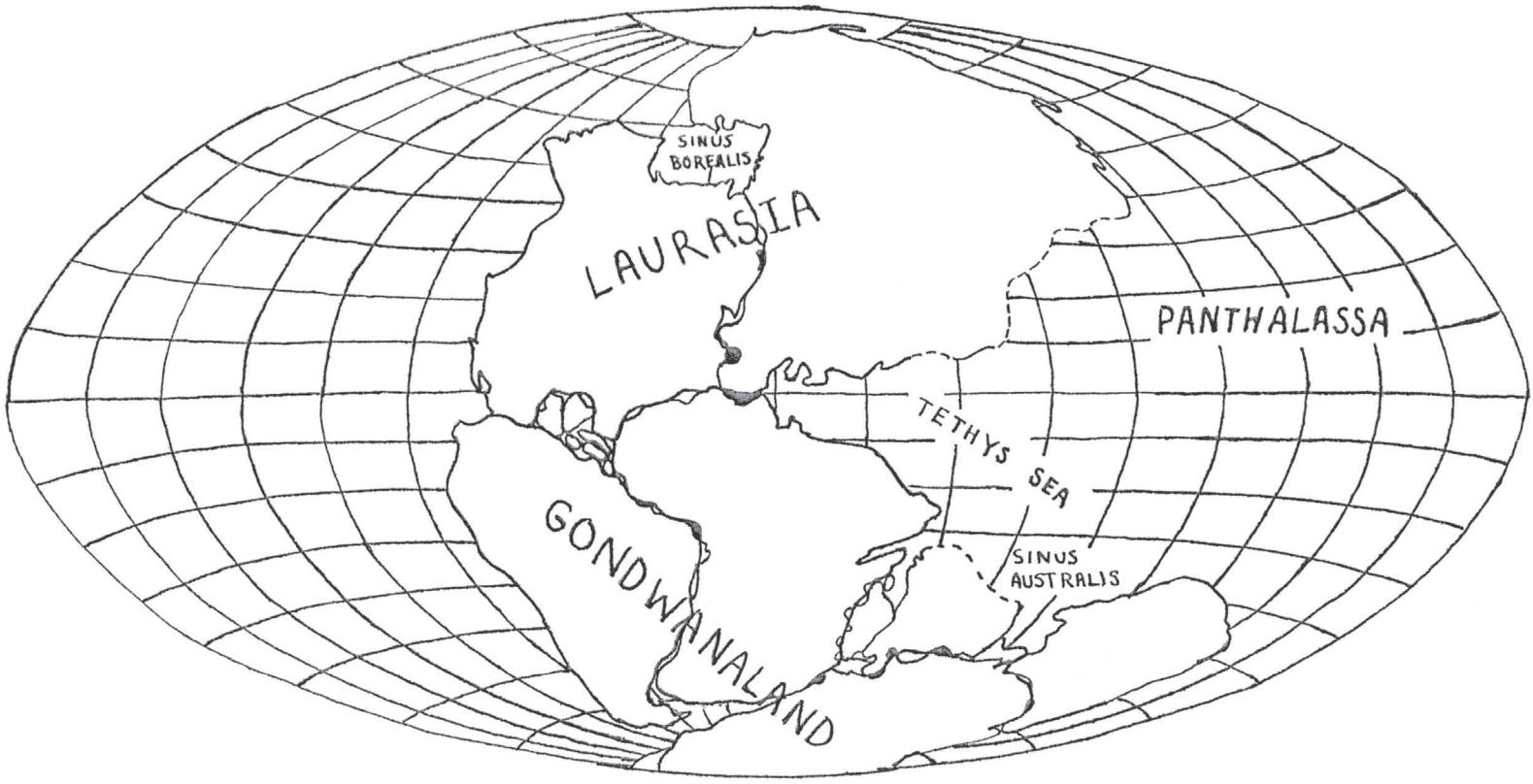

Fig.1. Paleogeography of Pangea (Dietz and Holden 1970).

Summary of the Forms of *Lystrosaurus*

Among the fossil anomondonts, hardly has there been any genus in which chance has played so much a part with regard to nomenclature as *Lystrosaurus*. Huxley (1859), who first described a member of this genus, called it *Dicynodon murrayi* without realizing that the specimen being described represented a new genus. Only a few months later, Owen (1859) independently described anomodonts akin to *D. murrayi* (Huxley) under a new generic name, *Ptychognathus*. It was soon discovered that this name had already been proposed for a crustacean (Brink 1951). Lydekker in 1890, therefore, proposed a new name, *Ptychosiagum*, for these anomodonts as a substitute for *Ptychognathus*. In the meantime, Cope in 1870 described another specimen akin to *D. murrayi* under the name *Lystrosaurus* with the result that the name *Lystrosaurus* received priority over *Ptychosiagum*. It was later shown that Owen's *L. declivis* and Cope's *L. frontosus* did not show any great differences from Huxley's *D. murrayi* (Broom 1932) and accordingly they were placed in synonymy with it.

Besides *L. murrayi*, the following new species of *Lystrosaurus* have been described by subsequent workers:

Ptychognathus declivis Owen 1859, South Africa.
Ptychognathus latirostris Owen 1859, South Africa.
Ptychognathus verticalis Owen 1859, South Africa.
Ptychognathus alfredi Owen 1862..
Dicynodon orientalis Huxley 1865, India.
Lystrosaurus frontosus Cope 1870, South Africa.
Ptychognathus boopis Owen 1876, South Africa.
Ptychognathus depressus Owen 1876, South Africa.
Dicynodon microtema Seeley 1889, South Africa.
Tropidostome dunni Seeley 1889, South Africa.
Dicynodon copei Seeley 1889, South Africa.
Rhabdocephalus maccaigi Seeley 1899, South Africa.
Mochlorhinus platyceps Seeley 1899, South Africa.
Lystrosaurus andersoni Broom 1907, South Africa.
Dicynodon strigops Broom 1913, South Africa.
Lystrosaurus putterelli van Hoepen 1915, South Africa.
Lystrosaurus breyeri van Hoepen 1916, South Africa.

Lystrosaurus jorrisseni van Hoepen 1916, South Africa.
Lystrosaurus jeppei van Hoepen 1916, South Africa.
Lystrosaurus theileri van Hoepen 1916, South Africa.
Lystrosaurus wageri van Hoepen 1916, South Africa.
Lystrosaurus wagneri van Hoepen 1916, South Africa.
Prolystrosaurus natalensis Haughton 1916, South Africa.
Lystrosaurus hedini Young 1935, China.
Lystrosaurus klimovi Efremov 1938, U.S.S.R.
Lystrosaurus weidenreichi Young 1939, China.
Lystrosaurus rubidgei Broom 1940, South Africa.
Lystrosaurus bothai Broom 1940, South Africa.
Lystrosaurus amphibius Brink 1951, South Africa.
Lystrosaurus primitivus Toerien 1954, South Africa.

For the first time, in 1890, Lydekker made an attempt to find out the validity of a number of species of Lystrosaurus proposed by Owen and others. He classed the then known species under five groups:

Ptychosiagum declive (Owen).

P. latirostris (Owen).
?P. alfredi (Owen).
?P. depressus (Owen).

Ptychosiagum microtema (Seeley).
Dicynodon (Tropidostoma) dunni (Seeley).

P. murrayi (Huxley).
P. vericalis (Owen).
P. boopis (Owen).
P. copei (Seeley).

P. orientale (Huxley).

In 1903, Broom placed two genera, Rhabdocephalus and Mochlorhinus, proposed by Seeley, in synonymy with Lystrosaurus. He admitted the validity of Owen's L. declivis and L. latirostris as different species. By 1932, Broom considered the Lystrosauridae by far the most difficult genera of South African fossil reptiles to deal with, and he admitted that this group was in great confusion. He then proceeded to revise the genus Lystrosaurus, referring some of the described species to Lystrosaurus murrayi. He admitted only the following four species which, according to him, were based on definite variations:

L. murrayi (Huxley).

L. platyceps (Seeley).

L. maccaigi (Seeley).

L. andersoni (Broom).

In the same paper, he also states "that where many specimens of the same genus are found at one locality and in one horizon the presumption should be that most will belong to one species, and that many distinct characters must be evident before a distinct species can be created." Unfortunately very little notice was taken of this advice, either by himself or by other workers on the genus Lystrosaurus (witness the above listings) or for that matter on various other genera of the mammal-like reptiles.

Brink (1951) again revised the twenty-two already described South African species of Lystrosaurus, reducing them to eleven and suggested that the generic name Prolystrosaurus should be altered to Lystrosaurus as the former is not a natural ancestor of the latter. He also provided a significant analysis of the lineage of the genus (fig. 2).

Neither of the above authors gave very definite reasons for reducing the number of the described species, but from a recent survey (Kitching 1968), it became evident that the majority of specimens were either badly preserved or distorted and some of them possessed no characteristics sufficiently distinctive to justify their separation into different species. With this consideration, Kitching (1968) reduces the species of Lystrosaurus to six, while Cluver (1971) feels that a reduction to nine is necessary. If those species upon which Kitching and Cluver agree are considered,, there are six valid species: Lystrosaurus murrayi (Huxley), L. declivis (Owen), L. curvatus (Owen), L. platyceps (Seeley), L. maccaigi (Seeley), and L. oviceps (Haughton). These may be placed within two general categories according to

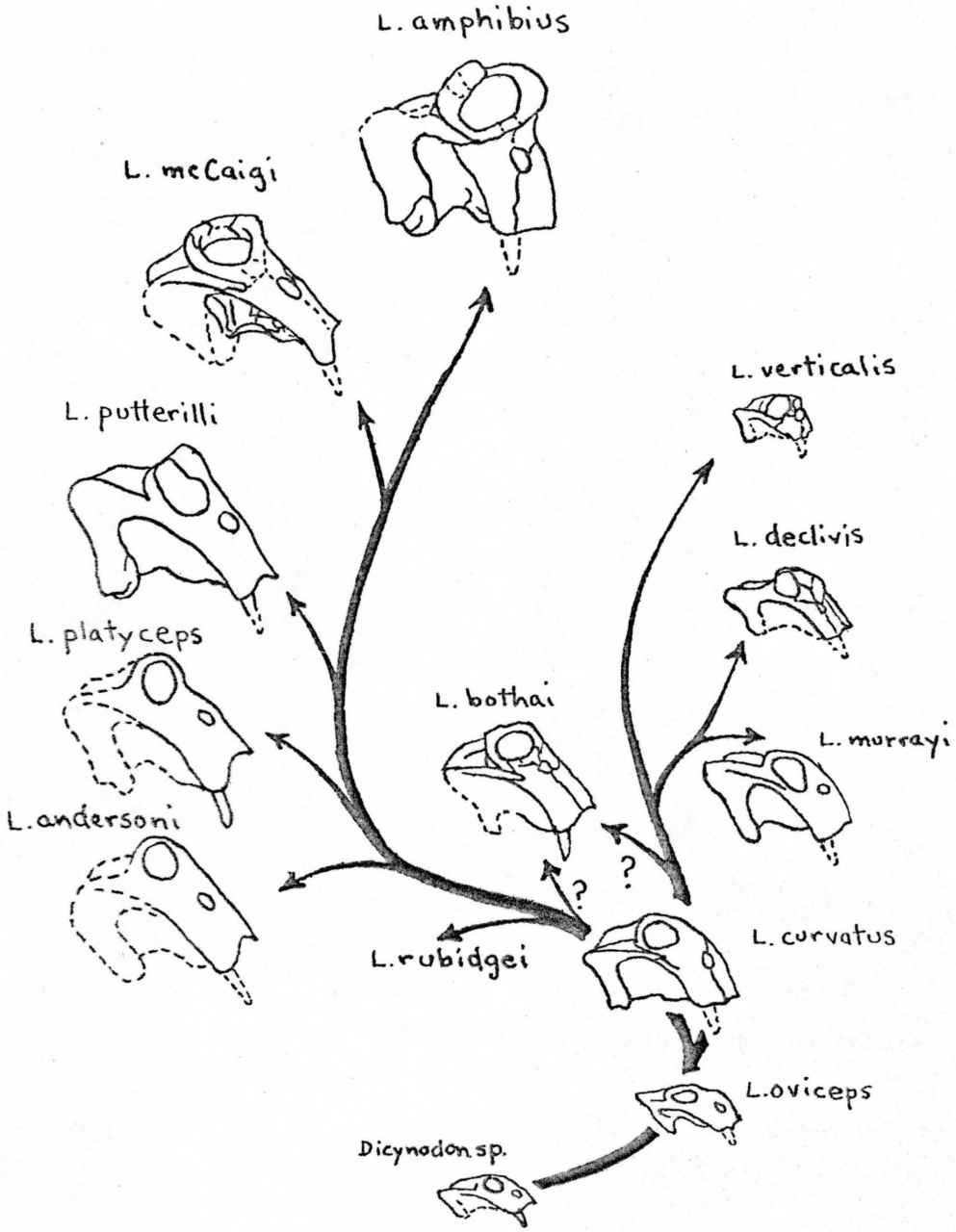

Fig. 2. Diagrammatic representation of the relationship between the different South African species of Lystrosaurus as presented by Brink (1951).

certain morphological features of the skull. In the first group, the skull has a strongly developed snout, the tusks are rather large, and there are well-developed cranial outgrowths on the skull (nasal ridges, tubercles, bosses and longitudinal ridges on the snout). Within this category may be included L. murrayi, L. mccaigi, and L. declivis (Cluver 1971). The second group is characterized by a moderately developed snout, generally smaller tusks, and smooth skull surfaces. Within this category may be included L. curvatus and L. platyceps. Lystrosaurus oviceps is somewhat intermediate in position. The dichotomy suggested perhaps represents sexual dimorphism in Lystrosaurus. Indeed, sexual dimorphism has been considered since the time of Owen in examinations of Lystrosaurus. However, Cluver (1971), after careful examination of the two lines of development, asserts that the dimorphism does not approach anything close to the fifty-fifty ratio that might be expected if sexual dimorphism did exist. It is therefore obvious that the dichotomous relation of Lystrosaurus species represents a split in the evolutionary development.

Given the above analysis, it seems that Lystrosaurus curvatus is the most primitive species of the genus (Colbert 1974). From such a form, Lystrosaurus evolved on the one hand into L. platyceps with many of the primitive characters retained. On the other hand, the species evolved into L. murrayi, L. mccaigi, and L. declivis, involving an elongation of the snout and a development of facial outgrowths on the prefontals, frontals, and nasal bones. Lystrosaurus oviceps may be a species on the way toward specialization, or it may be an intermediate form (Colbert 1974).

Description of Specimens

Stratigraphy

The collection of the specimens was made at three localities within the Shackleton Glacier area. These are Collinson Ridge, Thrinaxodon Col, and Mt. Kenyon (fig. 3). The fossils occurred in the lower 200 m of the 1000 m thick Fremouw Formation (Kitching, Collinson, Elliot, and Colbert 1972). The Fremouw Formation is composed of quartzose sandstone and interbedded noncarbonaceous mudstone beds totaling 75 to 125 m thick, and the overlying 530 m of greenish-gray and mudstone and light-colored sandstone (Barrett 1969). This lower portion of the Fremouw Formation consists of a cyclic unit of one to several fining-upward cycles typical of fluvial deposition (fig. 4). At the base of the cycle is a coarse channel conglomeratic sandstone, containing a minor quantity of disarticulated bones. Within the cycle, the sediments grade upward to medium and fine sandstone. Capping these sandstones are green-gray mudstones in which a more substantial quantity of bones are found. The erosional surfaces, mudstone fragments, trough cross-bedded sandstone and the fining upwards cycles found within the Fremouw indicate a floodplain environment of deposition. Root impressions and tree stumps demonstrate that vegetation grew in the area throughout the deposition of the formation (Barrett 1969). The Lystrosaurus specimens found at Collinson Ridge were located within the very fine sandstone and mudstone facies at various levels within the suggested stratigraphic column. The same can be said for those specimens found at Thrinaxodon Col. However, those found at Mr. Kenyon are contained in both the mudstone beds and the conglomeratic sandstone beds. The clasts that make up the conglomerate seem to be derived from older, fine-grained floodplain deposits. It is interesting to note a contrast in depositional features concerning the sediments associated

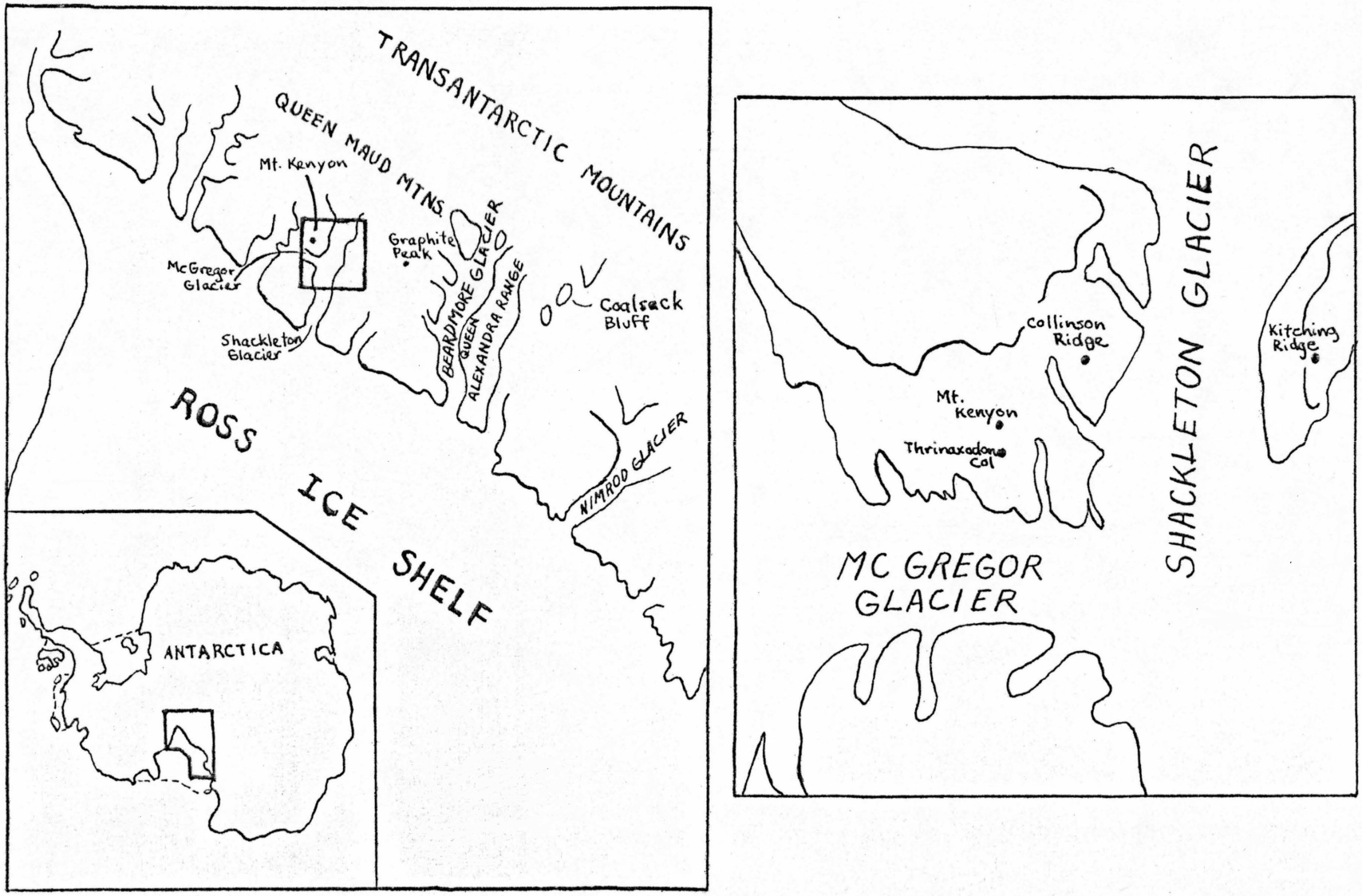

Fig 3. Shackleton Glacier Area, Antarctica (Kitching, Collinson, Elliot, and Colbert 1972).

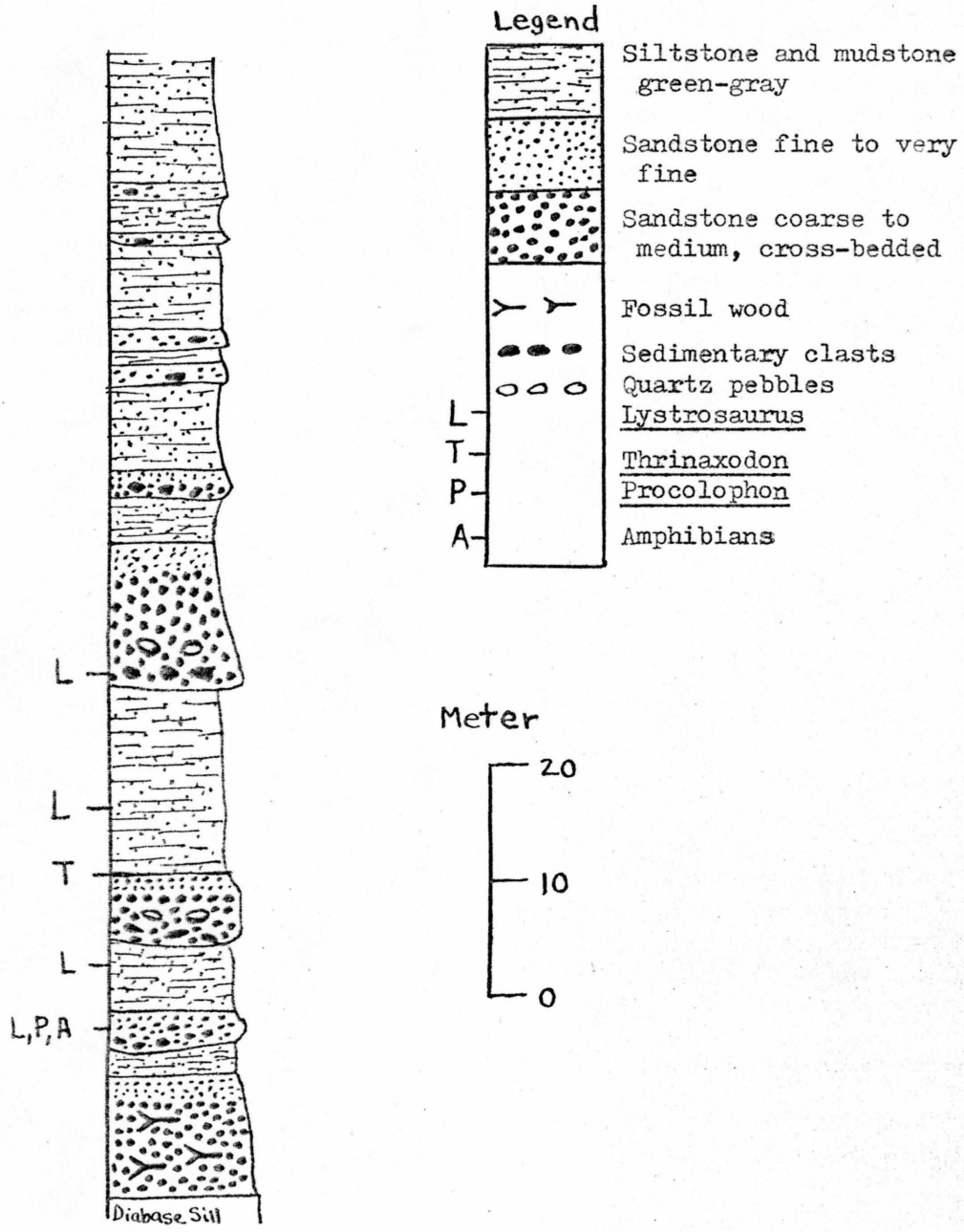

Fig. 4. Stratigraphic section of bone-bearing strata of the basal 100 m of the Fremouw Formation (From Kitching, Collinson, Elliot, and Colbert 1972).

with Lystrosaurus between those of Antarctica and South Africa. As mentioned above, the Antarctica bones are disarticulated, reflecting some transportation by stream action. However, those bones found in South Africa are articulated, buried in sediment that were accumulating in quiet ponds and slugish streams (Colbert 1970). The condition and disarticulated state makes the study of the bones found in Antarctica somewhat more difficult.

General Characters of the Specimens

The specimens are represented by a considerable number of ribs, a partial scapula, a nearly complete humerus, crushed radius and ulna, a number of undetermined foot bones, a femur, and a tusk. There is a singular lack of vertebrae and skull material, other than the one tusk. The cranial material was separated from the rest of the collection for other studies and does not appear here. It is probable that the specimens all represent the same genus, despite the fact that there is more than one animal represented by the specimens.

Preparation of the specimens consisted of work done on an air-abrasion unit. In exceptional cases, complete specimens were excavated from the matrix. However, due to the fragile condition and lateral compression of the bone material, most specimens were only partially prepared.

All specimens were in need of reconstruction, namely the proximal and distal heads of the humerus, the distal head below the acromion process of the scapula, the proximal and distal heads of the femur, and the heads of the radius and ulna.

Inspite of differences in the fossilization and matrix component, all the above described specimens represent a harmonic unit, in size as well as in structure.

They belong to the same form, most probably a Lystrosaurus.

Systematics

Phylum Chordata
Subphylum Vertebrata
Class Reptilia
Subclass Synapsida
Order Therapsida
Suborder Anomodontia
Infraorder Dicynodontia
Family Lystrosuridae
Lystrosaurus

(From Romer 1966)

The Pectoral Girdle

The pectoral girdle is represented by one scapula only (fig. 5). It is a nearly complete left scapula, fractured slightly above the acromion process so that the process and glenoid are missing. However, reconstruction is considerably eased when comparing the general shape with that given for another Lystosaurus species (Watson 1913). The acromion process is situated closely to the distal end, forming a sharp and narrow embayment with the wing-like process anterior to the glenoid fossa. The part above the acromion process is slightly convex on the external side and rather deeply concave on the internal side. The posterior border of the bone is almost straight and there is no marked curvature in the middle part of the bone. There is no remarkable palmation of the proximal portion. Maximum length of the specimen, 32 mm; maximum reconstructed length 67 mm; maximum proximal breadth 26 mm; reconstructed distal breadth, 25 mm; minimum breadth above the acromion process, 13 mm.. Horizon and locality: 190 m above basal Fremouw, Collinson Ridge. Specimen number 31402 (Orton Geology Museum). Collected by J. W. Collinson, Department of Geology, The Ohio State University.

The scapula in Lystrosaurus bears a close resemblance to that bone in Cudenodon and Dicynodon (Broom 1903). The general view is that the upper part of the blade is broad and moderately flat from side to side. A little

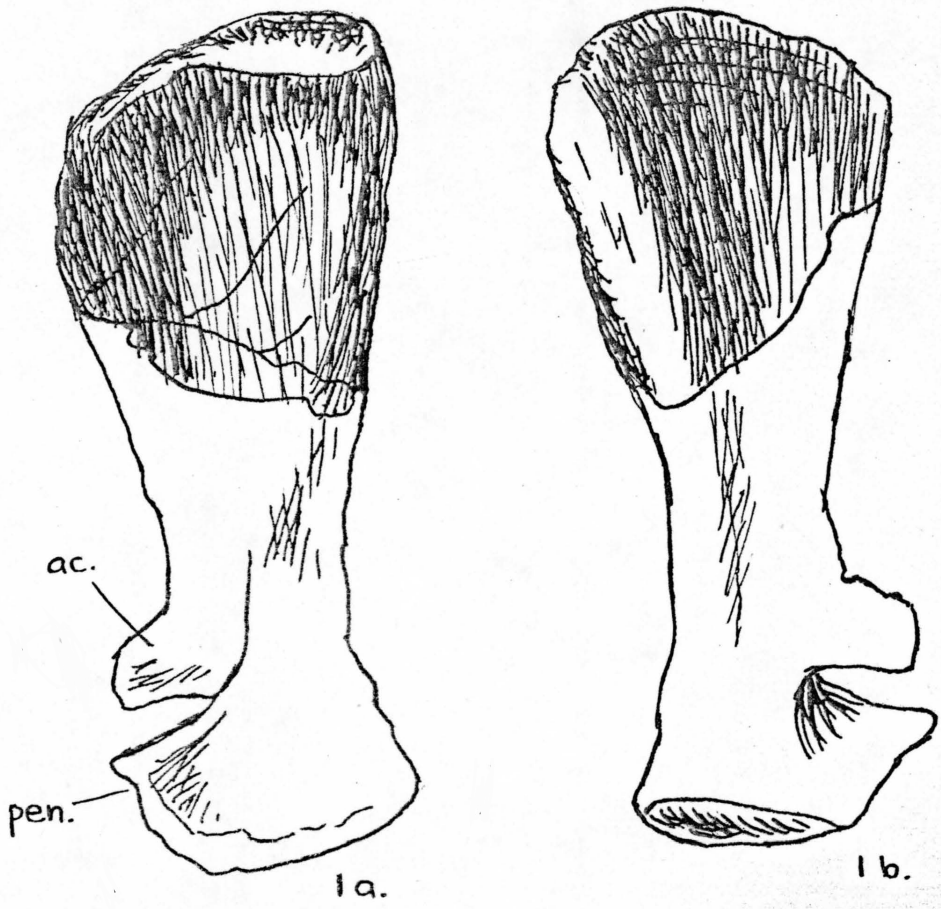

Fig. 5. Left scapula, internal view; 1a. external view; 1b. ac. acromion process; pen. notch for precoracoid foramen. X 2.0. Specimen number 31402 (Orton Geology Museum).

below the middle of the bone there is a well-developed acromion process anteriorly. It may be described as a triangular plate which, on passing forwards, is directed slightly inwards from the plane of the general surface of the scapula. The lower part of the scapula is considerably broader than in Cudendon. The posterior part of the lower end forms probably half of the large glenoid cavity. The anterior expansion of the lower end passes further forward than the acromion and forms a long articulation with the precoracoid. It is notched to form part of the precoracoidal foramen.

The shoulder girdle in Lystrosaurus is interesting as a specialized variety of the Anomondont type. Among both mammals and reptiles we find instances of the remarkable modifications in the shoulder girdle that may follow the adoption of a purely aquatic life. Thus in the Pythonomorpha, the clavicles and interclavicles become quite rudimentary or entirely lost, and in whales the clavicles disappear. In the plesiosaurians both the clavicles and interclavicle become greatly reduced and the interclavicle may disappear. In ichthyosaurians, though, the clavicles are moderately well developed, the interclavicle is usually small.

It would therefore seem probable that the reduction of the interclavicles, the increase in size of the sternum, and precoracoid have been brought about by the aquatic habits of Lystosaurus (fig. 6). Unfortunately, only the partial scapula can be discussed in conjunction with these specimens. It is hopeful that a reconstruction based on the present scapula and associated structures described by Broom (1903) will lend to a better understanding of the habits of Lystrosaurus and the implications discussed later concerning continental drift.

Finally, it is impossible to determine the species position of the Lystrosaurus specimen by the incurved method of the scapula as suggested by Young (1939) in that the scapula of the specimen is incomplete and all

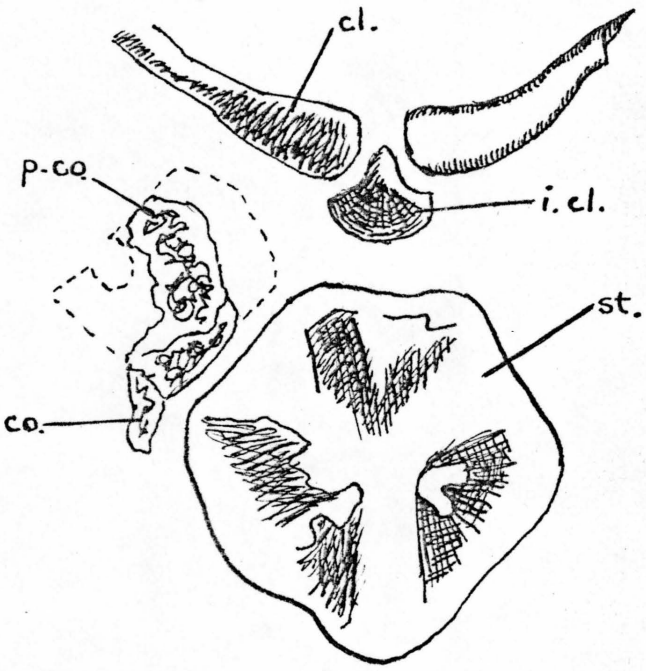

Fig. 6. Sternum, clavicles, interclavicle, precoracoid and portion of coracoid of Lystrosaurus (From Broom 1903). cl. clavicle; co. coracoid; i. cl. interclavicle; p. co. precoracoid; st. sternum.

specimens show distortion (lateral compression) which would tend to mask any curvature of a plate-like bone such as a scapula.

Fore Limb

The fore limb is represented by the left humerus and the right radius and ulna. There are a few phalanges; however, they are very distorted and hence indistinguishable. The absence of carpals is perhaps due to a cartilaginous state.

The humerus (fig. 7) is exceptionally complete, especially when compared with the condition of the other specimens. The general shape of the bone is massive, chiefly due to the large development of the deltoid crest (partially absent in specimen) and to the enormous expansion of the distal end. The arterior view indicates that the upper part of the bone is marked by a strong concavity due to the turning and curving of the deltoid crest. In the posterior aspect, the corresponding part is convex. The constriction of the bone in the middle is very strong. Maximum length, 56 mm; maximum proximal breadth, 28 mm; maximum distal breadth, 39 mm; minimum breadth of the shaft, 14 mm. Horizon and locality: 315 m above basal Fremouw, Collison Ridge. Specimen number: 31401 (OGM). Collected by J. W. Collinson, OSU.

The radius and ulna are of the general shape of the usual dicynodontian type. They are preserved as a pair, both extremely laterally compressed, as is common with all of the specimens, and there was considerable reconstruction necessary, as both proximal and distal heads were not extant. However, the radius is a short bone, with a narrow, nearly circular, shaft, expanded at the top to a head. The lower end is much expanded laterally. The ulna has a stout head of triangular section whose inner face articulates with the head of the radius. There is no prominent olecranon process, but the bone obviously had a cartilaginous expansion in this region (Watson 1913). The shaft is thin

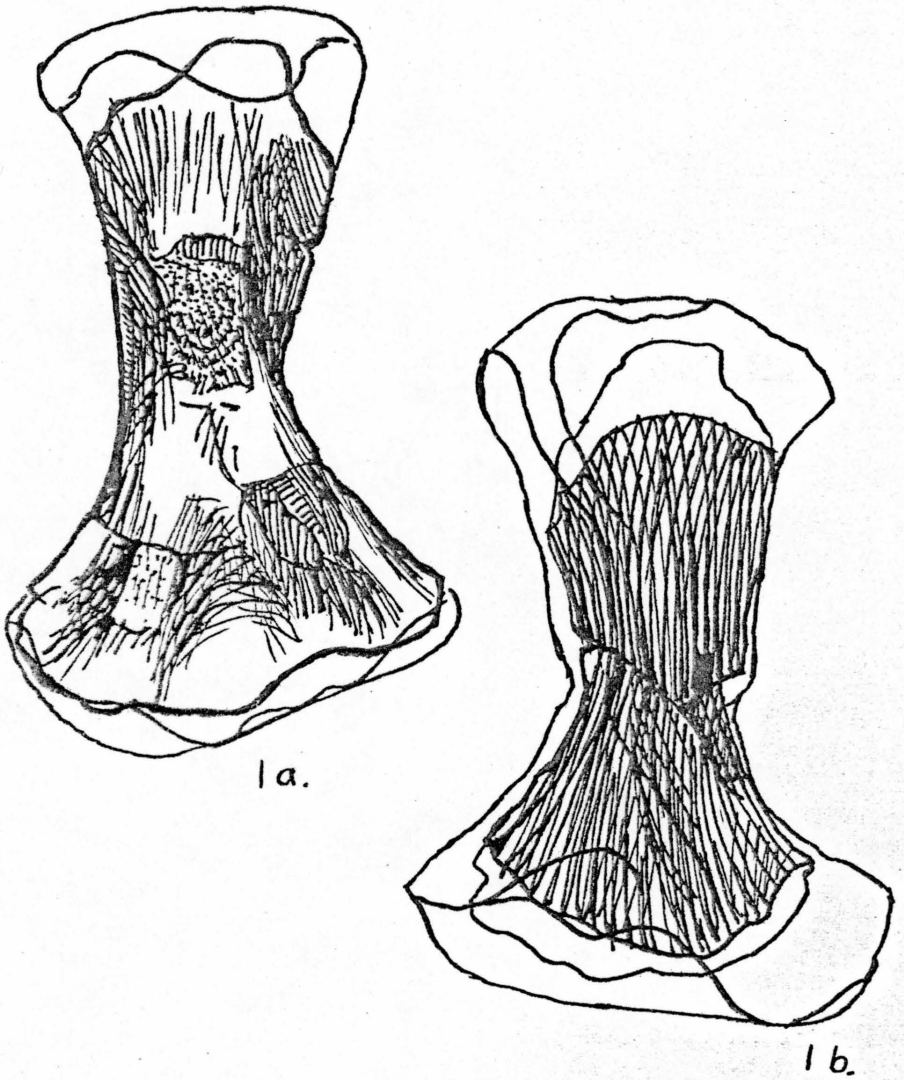

Fig. 7. Anterior (1a) and posterior (1b) views of the right humerus. X 1.6. Specimen number 31401 (OGM).

and the lower end is laterally widened (fig. 8). Ulna: maximum reconstructed length, 51 mm; maximum reconstructed proximal breadth, 25 mm; maximum reconstructed distal breadth, 14 mm; minimum breadth of the shaft, 8 mm. Radius: maximum reconstructed length, 45 mm; maximum reconstructed proximal breadth, 15 mm; maximum reconstructed distal breadth, 21 mm; minimum breadth of the shaft, 8 mm. Horizon and locality: 242 m above basal Fremouw, Collinson Ridge. Specimen number: 31406.(OGM). Collected by J. W. Collinson, O.S.U.

As in all Anomodonts, the forearm was carried at right angles to the humerus and probably had only a very limited range of movement (fig. 9). Studies of well preserved shoulder girdles show that the humerus was carried generally at right angles to the body, as in most primitve reptiles and living monotremes (Watson 1913).

Ribs

A large number of ribs are represented, some being fairly complete (fig. 10). The proximal end of the bone is clearly expanded in the anterior ribs, and there is separation observable between the tuberculum and capitulum. Horizon and locality: 295 m above basal Fremouw, Collinson Ridge. Specimen number: 31405 (OGM). Collected by J. W. Collinson, O.S.U.

Hind Limb

Of the hind limbs, only the left femur has been preserved. The proximal head and distal articulation have been destroyed and subsequent reconstructions compensating for the imcompeteness and lateral compression are based on Broom (1932). No trace of any bone might be refered to the tibia, fibula, tarsus, metatarsus, or phalanges.

The femur is incomplete, as stated above, and consists of a slender shaft with a considerable expansion toward the proximal end. In the recon-

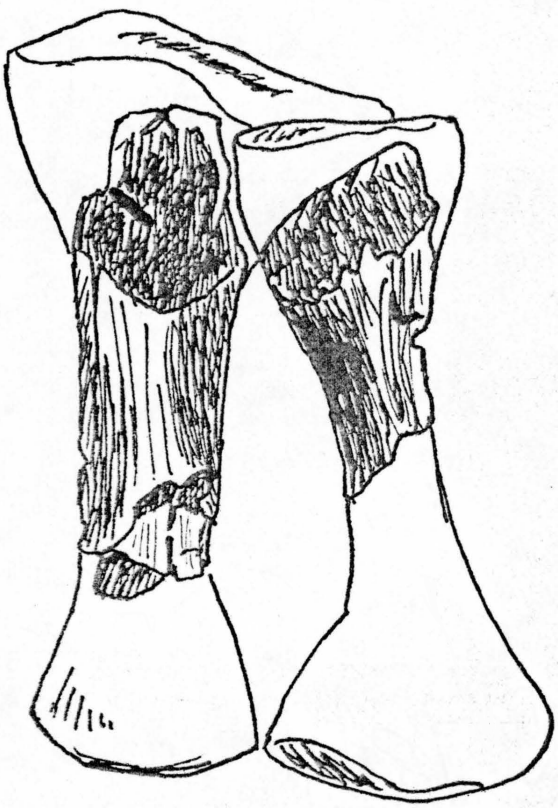

Fig. 8. External view of right ulna and radius. X 2.0.
Specimen number 31406 (OGM).

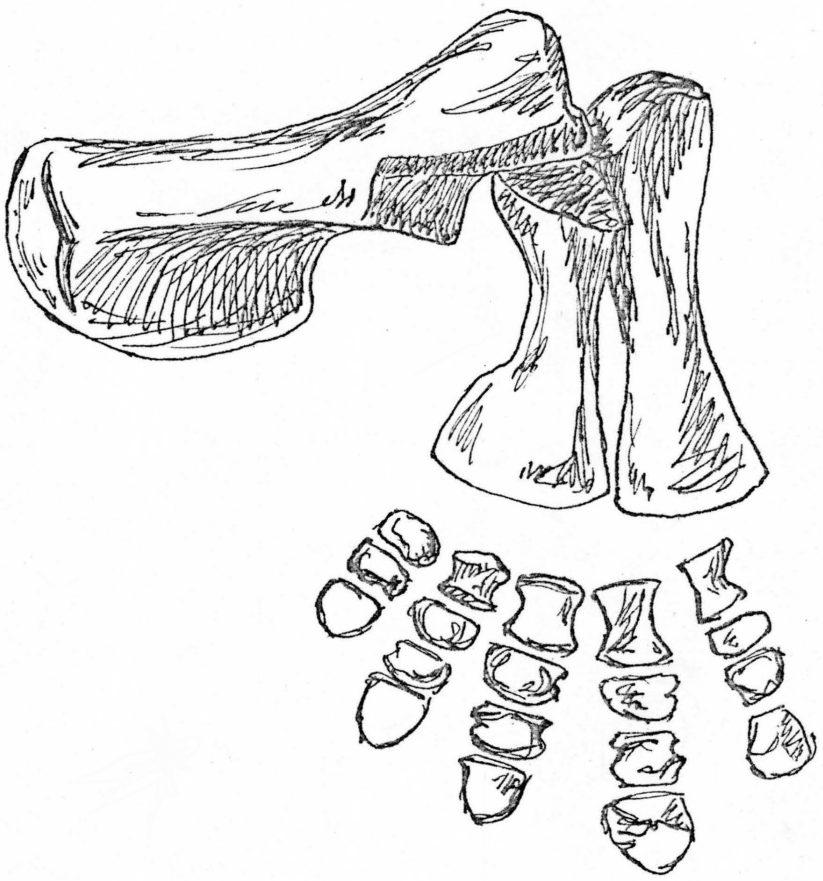

Fig. 9. Left forearm of Lystrosaurus, viewed from the front. The lower end of the humerus is broken so as to show the articular face of the upper end of the radius. (From Watson 1913).

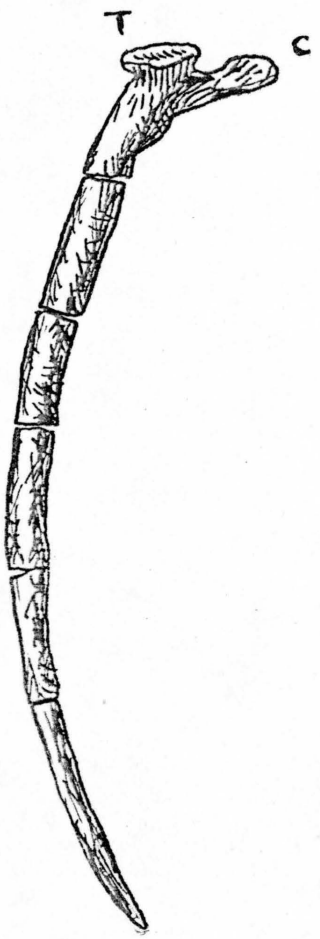

Fig. 10. Rib of anterior region. C, Capitulum. T. Tuberculum. X 2.0. Specimen number 31405 (OGM).

structed model (fig. 11), it can be seen that the distal end was expanded as well. The trochanter major is seemingly well developed and there is no trace of the internal trochanter. In the reconstruction, the distal expansion is almost symmetrical with a broad end necessary for the articulation with the tibia and fibula. Total length of the specimen, 51 mm; total reconstructed length, 76 mm; maximum reconstructed proximal breadth, 29 mm; maximum reconstructed distal breadth, 27 mm; minimum transversal breadth, 9 mm. Horizon and locality: 242 m.above basal Fremouw, Collinson Ridge. Specimen number: 31403.(OGM). Collected by J. W. Collinson, O.S.U.

Tusk

The preserved tusk is oval in cross section. It has seemingly been broken near the root area. There seems to be no markings such as longitudinal grooves. When articulated with the skull, the tooth ran parallel with the axis of the muzzle (fig. 12). There is a facet of wear on what would be the lingual side of the tusk. Mean diameter of the tooth, 12.5 mm. Horizon and locality: 315 m above basal Fremouw, Collinson Ridge. Specimen number: 31404 (OGM). Collected by J. W. Collinson, O.S.U.

Dimensional Comparison of the Lystrosaurid Specimens and Lystrosaurus

Throughout the history of Lystrosaurian investigations, there has been a singular lack of postcranial studies. The importance of such a study is obvious, when presented with skull-less specimens, in order to substantiate the taxonomic position. It is also important to develop an idea of the mode or modes of locomotion of the Lystrosaurians. The former will be treated first, while the latter will be discussed with the implications of the occurrence of Lystosaurus in Gondwanaland.

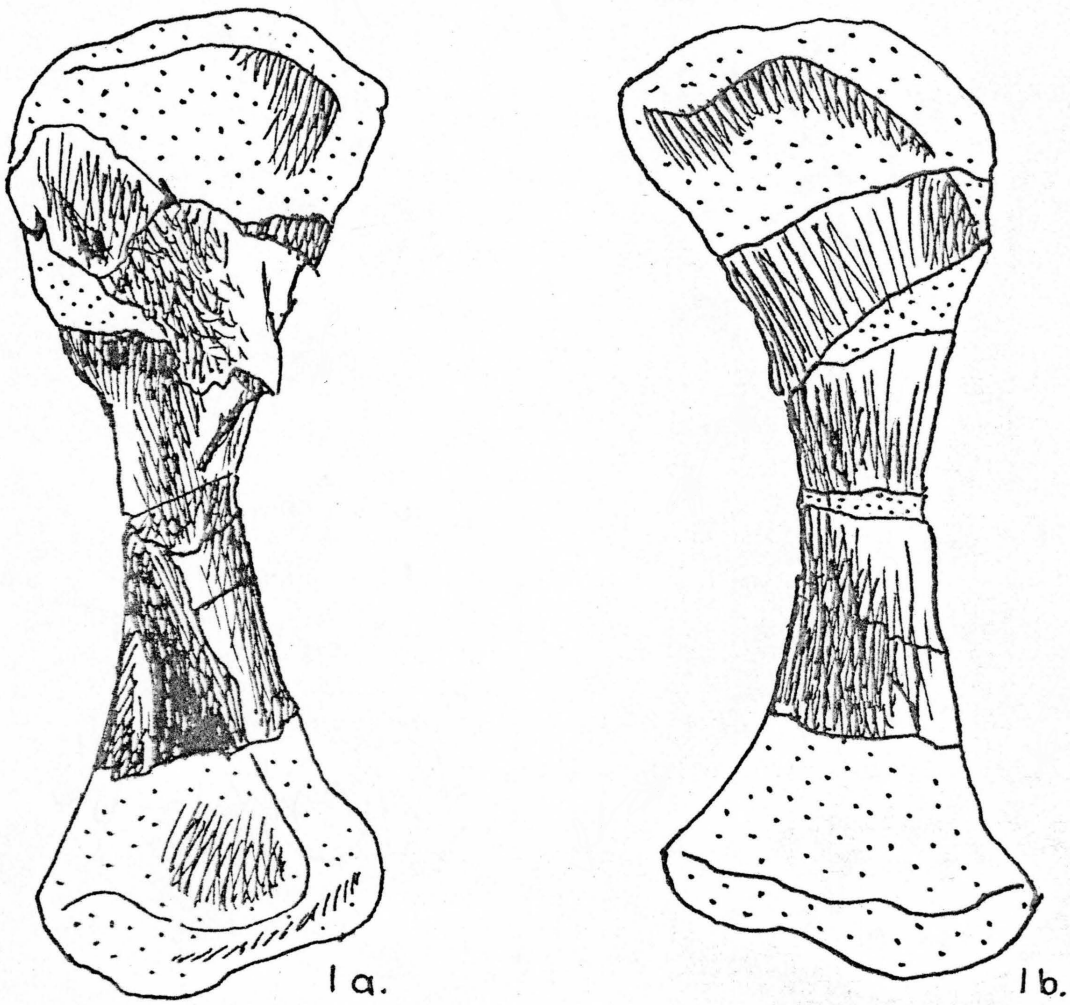

Fig. 11. Anterior (1a) and posterior (1b) views of left femur. X 2.0. Specimen number 31403 (OGM).

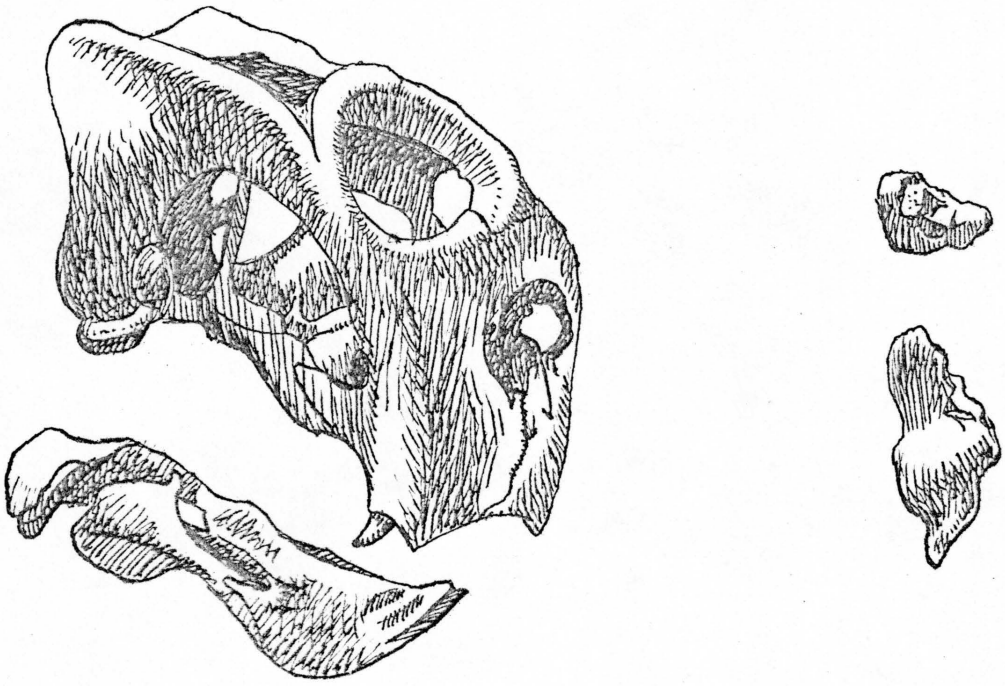

Fig. 12. Skull and tusk of Lystrosaurus. Tusk X 2.0.
Specimen number 31202 (OGM).

The most practical and most significant manner to make a generic detemination of a taxon from specimens which do not exhibit diagnostic characteristics is to investigate the dimensional comparisons between the unspecified specimens and the known genus. The dilemma of Lystrosaurus, with its cranial diagnosis, can be resolved in the above manner by a determination of the ratios between complementary dimensions of the specimens and a postcranially known Lystosaurus, L. hedini (Young 1935). Given an accurate determination of this ratio, it is possible to apply the concept of standard deviation to find how the specimens comply with the expected result as determined through the known Lystrosaurus. The results appear in Table 1. It can be seen that 50% of the dimensions found from the specimens are within 1 standard deviation unit and all of the dimensions agree with those determined by Young (1935) within 1.45 standard deviation units. From these calculations, it can be seen that the specimens, despite the lack of cranial characteristics, agree to a high degree with those of a known Lystrosaurus, and therefore it is highly likely that the specimens are members of the genus Lystrosaurus.

The comparison of dimensions indicate a 50% reduction in size of all specimens compared with L. hedini. Such a relation suggests that the specimens represent immature examples of Lystrosaurus. Why all specimens exhibit this immature condition is not known. However, such a close dimensional comparison coupled with a strong degree of resemblence between the specimens and known forms is enough to dismiss any notion of the specimens representing a different taxon. If indeed these specimens represent true immature Lystrosaurians, then what of allometric growth? It is especially notable that in humans the immature members have significantly different body proportions than adults, and that during the life history of that member, the arms and legs grow at a faster rate than the head. This is allometric growth. In dealing with

Table 1.

	Dimensions:	*Lystrosaurus* sp.	*Lystrosaurus hedini*	Ratio	Mean	$\Delta(\bar{x} - x)$	$(\bar{x} - x)^2$	s^2	s	x/s
Scapula	Maximum length	67 mm	122 mm	.549	.533	.016	.000256	.000648	.0255	.6274
	Proximal breadth	26 mm	49 mm	.530	.533	.003	.000009	.000648	.0255	.2353
	Distal breadth	25 mm	50 mm	.500	.533	.033	.001089	.000648	.0255	1.2941
	Minimum breadth below acromion process	13 mm	26 mm	.500	.533	.033	.001089	.000648	.0255	1.2941
Humerus	Maximum length	56 mm	112 mm	.500	.533	.033	.001089	.000648	.0255	1.2941
	Proximal breadth	28 mm	53 mm	.528	.533	.005	.000025	.000648	.0255	.1961
	Distal breadth	39 mm	78 mm	.500	.533	.033	.001089	.000648	.0255	1.2941
	Minimum breadth of shaft	14 mm	26 mm	.538	.533	.005	.000025	.000648	.0255	.1961
Ulna	Maximum length	51 mm	91 mm	.560	.533	.027	.000729	.000648	.0255	1.0588
	Proximal breadth	25 mm	44 mm	.568	.533	.035	.001225	.000648	.0255	1.3724
	Distal breadth	14 mm	26 mm	.538	.533	.003	.000009	.000648	.0255	.2353
	Minimum breadth of shaft	8 mm	14 mm	.571	.533	.037	.001369	.000648	.0255	1.4509
Radius	Maximum length	45 mm	79 mm	.569	.533	.036	.001296	.000648	.0255	1.4117
	Proximal breadth	15 mm	30 mm	.500	.533	.033	.001089	.000648	.0255	1.2941
	Distal breadth	21 mm	40 mm	.525	.533	.008	.000064	.000648	.0255	.3137
	Minimum breadth of shaft	8 mm	14 mm	.551	.533	.018	.000324	.000648	.0255	.7058
Femur	Maximum length	76 mm	145 mm	.524	.533	.009	.000081	.000648	.0255	.3529
	Proximal breadth	29 mm	55 mm	.527	.533	.006	.000036	.000648	.0255	.2353
	Distal breadth	27 mm	53 mm	.509	.533	.024	.000576	.000648	.0255	.9411
	Minimum breadth of shaft	9 mm	16 mm	.562	.533	.029	.000841	.000648	.0255	1.1372

immature Lystrosaurians, it becomes important to recognize any allometry which may exist. Unfortunately, there has been no work in this area to date. However, Romer (1956) notes that in general reptiles exhibit no pronounced allometric growth. It is therefore most probable that the specimens represent immature examples at one-half the body size of an adult.

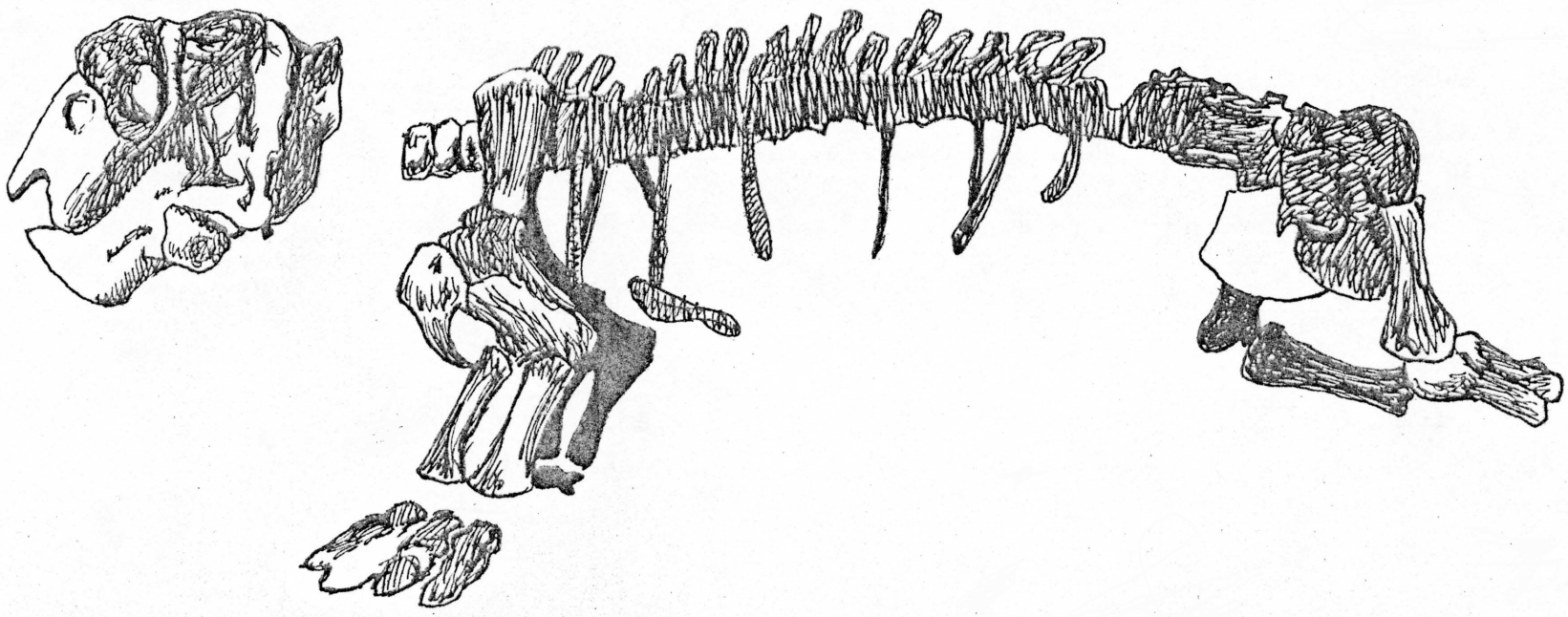

Fig 13. Entire Articulated Skeleton of Lystrosaurus hedini. X .16.
(Modified from Young (1935)).

Implications of Lystrosaurus on Continental Drift

The presence of Lystrosaurus in the Lower Triassic Fremouw Formation of Antarctica, in the Panchet Formation of India, in the Karroo sequence of South Africa, and the lower Triassic sediments of China constitutes strong evidence indicating the strong ligation of these widely separated continents. The implications of these considerations with regards to Gondwanaland and continental drift are of prime importance. The analysis of the various forms of Lystrosaurus has yielded an accurate phylogeny of the genus and as such, an evaluation of the spacial occurrences as compares with speciation can be made.

The obviously primitive L. curvatus and L. murrayi are the most widely distributed of the species, being found in Africa, Asia, and Antarctica. Perhaps these two species represent an initial radiation of Lystrosaurus through Gondwanaland, whereas the other species represent later specializations, locally developed.

Lystrosaurus murrayi in Africa, Antarctica, and peninsular India, L. curvatus in Africa and Antarctica, and L. mccaigi and L. platyceps in Africa and India, lend strong support to existing physical evidence to the ligation of these land masses as part of a Gondwana continent during early Triassic time. The Lystrosaurus material found within the Fremouw Formation includes other fossil forms--Thrinaxodon, Procolophon, thecodonts, and labyrinthodonts. This assemblage points to a fauna that duplicates to an uncanny degree the typical South Africa assemblage. In spite of the distance involved between South Africa and peninisular India, the resemblence between Lystrosaurus in these two regions seems to be fully as close as between the Antarctic and African fossils (Colbert 1971). Consequently it seems reasonable to think that Lystrosaurus in India lived in close communication with

Lystrosaurus in Africa. If one accepts the probable reality of a Permo-Triassic Gondwanaland with its now separated segments fitted together in the manner outlined by Dietz and Holden (1970), then the distribution of a major part of the Lystrosaurus fauna assumes a very interesting and reasonable pattern. The occurrences of this fauna in Antarctica, Africa, and India, instead of being separated each from the other by distances of many thousands of miles, are brought into spacial relationships of continental proportions. The problem posed by the occurrence of Lystrosaurus in Indo-China and China can perhaps be answered in two ways. Recent evidence seems to indicate that Indo-China may have once been a part of the Gondwanaland continent, situated between the Indian peninsula and Australia. Such a positon would explain the presence of Lystrosaurus in present-day southeastern Asia. The presence of Lystrosaurus in Shansi, and especially in Sinkiang, can also be explained on the basis of an original Gondwanaland distribution, if one is willing to accept the inclusion of much of China within Gondwanaland, as recently has been tentatively suggested by Hurley (1971). Alternatively, one must suppose that Lystrosaurus arrived in the northeastern part of Asia by a long intercontinental migration from its original homeland--northward through the African portion of Gondwanaland, into Laurasia at the Spanish "hinge" (the Spanish-Moroccan region that served as a connection between the super-continents), and from there to the east into what now is northwestern and central China.

It is important to understand that the occurrence of Lystrosaurus throughout the Sout African and Antarctican portion of Gondwanaland as exemplified by the existence of the primitive forms there, is not one of a mighty migratory nature as suggested by Kitching (1968). He states that the abundance of Lystrosaurus through the Lower Beaufort Zone is more indicative

of an immigrant form, than one evolved from a branch of the Anomodonts. However, as shown by the forms in Antarctica, it seems clear that the abundance is a result of environmental conditions. It is as though the consequences of evolutionary proliferation in conjunction with beneficial envircns allowed Lystrosaurus to propogate in quantity. Such a concept is rooted in the locomotory mode of the animal. It is important to evaluate whether the occurrence of Lystrosaurus is correlative with an aquatic habit as suggested by Crompton (1971). The wide distribution of fossils of this genus might be accounted for by the fact that, being able to swim, these creatures occupied areas (flood plains) typified by depositional processes. They would have been deposited by streams or floods with many surviving whole, but some being dismembered, giving rise to the skull and skeletal fragments in the pebble conglomerates, as has been mentioned in consideration of the dichotomous depositional qualities between South Africa and Antarctica. It is conceivable that, over geologic time, the effects of evolutionary proliferation coupled with evidence of the remains of known primitive forms tend to obscure any migratory concept. Thus, in South Africa and Antarctica, it appears that the suggested aquatic habit and associated fluvial deposits are the mechanisms for the abundant remains. However, for this statement to be completely reliable, it is extremely important to investigate the postcranial elements. Thus far, this has not been done. It has been suggested that Lystrosaurus had a similar habit as that of the hippopotamus, as dictated from the placement of the nares and orbits (Brink 1951). It would be more important to determine the extent to which the limbs and body cross-section comply with that of a hippopotamus. In this manner, it can be determined the hydraulic efficiency with which the animal could have used to locomote itself and as such, is a much better means of making a determination of any aquatic mode. The incompleteness of the specimens examined here unfortunately

hindered any such study for the present time.

Given an aquatic habit, Lystrosaurus would still be bound to terrestrial substrates as suggested by the fluvial floodplain deposits in which it is found. There can be no question that any aquatic migration from an isolated land mass to another is precluded from any possible migratory possibilities of Lystrosaurus. Therefore, the Lystrosaurian distribution described from South Africa, Antarctica, and India, is completely independent of any migrational considerations, other than terrestrial. Such a terrestrial mode is only important in the migrational consideration of the Lystrosaurus occurrence in western China, as mentioned above.

The elimination of most overland and all transoceanic migrations of Lystrosaurus and its associated fauna indicates that the regions in which they now occur were, during the Lower Triassic, joined in a way that the faunas were able to intermigrate within the aligned region. As such, the present theory of continental drift is in concordance with the zoogeography of Lystrosaurus. On the one hand, there does seem to be accordance between the phenomenon of an earth history involving a late Paleozoic and early Mesozoic Gondwanaland and Laurasia (or Pangea), the subsequent rifting of these land masses, and the ensuing drift of their component parts to the positions occupied by our modern continents, and on the other hand, of the distributions of tetrapod faunas through time. Given such a relationship, it is extremely important that Lystrosaurus and its associated fauna become an important tool in developing a realistic concept of the paleozoogeography of the Lower Triassic times. In doing this, all aspects, both phylogenic and ecological, must be analyzed in order to make any sort of distinction within a reconstruction of ancient land masses. Once these considerations have been dealt with, the significance of Lystrosaurus will provide information regarding a world profoundly different from the world with which we are familiar.

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